Energetic dynamics and anuran breeding phenology: insights from a dynamic game

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We designed a dynamic optimization model to examine anuran-breeding phenologies. We evaluated the fitness consequences for males adopting one of four alternative strategies: calling, satelliting, foraging, or hiding. Various factors potentially influence male behavior, including energy reserves, predation risk, cost of calling, probability of finding food, distribution of male energy states in the population, and probability of surviving to another breeding season. We manipulated these parameters to determine how strongly each affects breeding phenology and chorus structure. Manipulating parameters related to the energetic costs and benefits of individual decisions, we generated the three basic patterns of anuran breeding phenology: explosive, continuous, and prolonged breeding with episodic chorusing. Increasing the probability of successful foraging caused a shift from an explosive pattern to a prolonged, episodic chorusing pattern. Decreasing the calling cost resulted in continuous chorusing. Our model predicted that satelliting will be a rare strategy adopted by individuals with relatively low energy reserves. Additionally, individuals adopting the satellite strategy should alternate among satelliting, foraging, and calling as their energy reserves fluctuate. Our results suggest that energetic costs of reproduction and resource limitation may be crucial factors influencing the phenology of anuran chorusing. We propose that under varying conditions of resource availability, male decisions are the consequence of two strategies: a starvation minimization strategy and an energy-state maximization strategy. *Key words:* alternative mating strategies, anuran breeding, breeding phenology, chorusing, dynamic optimization modeling, leks.

Temporal patterns of anuran breeding activity are highly variable between and occasionally within species. This level of variation makes anurans an especially suitable system for testing hypotheses about ecological and evolutionary forces affecting reproductive strategies. Anuran breeding seasons can be generally classified as either explosive or prolonged. Although the length of the breeding season actually represents a continuum, those animals that breed for 1–14 days are generally considered explosive breeders, whereas prolonged breeders may breed anywhere from 1 month to throughout the entire year (Wells, 1977). Whereas explosive breeding seasons typically consist of continuous calling, prolonged seasons often involve a series of synchronous calling bouts alternated with periods of relative quiescence (Donnelly and Guyer, 1994; Green, 1990; Tejedo, 1992; Wagner and Sullivan, 1992). However, a few species of prolonged breeders have continuous chorusing throughout their entire breeding season. Continuous chorusers include species in which individual male participation is also continuous (Given, 1988) and species in which individual males have abbreviated chorus tenures within a continuous season (Bevier, 1997a; Murphy, 1994). Although these species have similar seasonal breeding phenologies, the differences in individual male behavior suggest that the factors influencing the development of continuous chorusing may vary between species. Understanding this variation will help us explore the general mechanisms important in structuring reproductive strategies.

Anuran breeding patterns have received significant theoretical and empirical attention, and several hypotheses have been proposed to explain the existence of prolonged and explosive breeders both within and among species. For many explosive breeders, the length of the breeding season may be limited by environmental conditions and the availability of suitable breeding sites (Sullivan, 1982b; Wells, 1977). Empirical and theoretical work also suggests that explosive breeding may be the result of increased predation pressure on a population (Lucas et al., 1996; Woodward and Mitchell, 1990), or it may serve to decrease egg and tadpole cannibalism by conspecifics (Petranka and Thomas, 1995). Finally, empirical evidence suggests a trade-off between the level of energy investment in calling on a single night and explosive or continuous chorusing patterns (Bevier, 1997a).

Several hypotheses have been proposed to explain the episodic bouts of calling by prolonged breeders. For example, calling periods may be associated with specific environmental conditions, such as rainfall (Green, 1990). In other species, hormonal cycles produce episodic breeding activity (Obert, 1977). In addition, because calling is typically considered energetically expensive (reviewed in Pough et al., 1992; Taigen and Wells, 1985; Taigen et al., 1985; Wells and Taigen, 1989), males may periodically cease calling to conserve energy (Grafe, 1997; Grafe et al., 1992; Schwartz et al., 1995). The relative importance of these factors may differ between species or populations.

We constructed a dynamic optimization model to explore the selection pressures that may have been important in the evolution of existing reproductive strategies. It is difficult to manipulate breeding phenologies experimentally or to obtain historical information on factors that contributed to the evolution of these reproductive strategies. Modeling these conditions allowed us to explore outcomes of multiple ecological and social forces and how they interact to produce a species' or a population's breeding phenology. Our model assumed an environment in which all days were equally suitable for breeding in order to evaluate explicitly whether energetic

Table 1
Cost and benefit parameters associated with each male tactic

Tactic (i)	Survivorship (s_i)	Energy cost (c_i)	Probability of finding food (f)	Foraging yield (y)	Mating success (MS_i)
Hide	1	1	0	0	0
Forage	0.99	1	0.4 (0.1–1.0)	2 (2–15)	0
Satellite	0.99	1	0	0	(see Methods)
Call	0.95 (0.81–0.99)	2 (1–2)	0	0	(see Methods)

Default values are presented, and the range of values explored for a given parameter is included in parentheses.

constraints could generate episodic or explosive calling bouts under environmentally favorable conditions.

In addition to variation in temporal chorusing patterns, we were interested in factors affecting male behavior within the chorus. Within choruses in which females have the opportunity for mate choice, males may adopt one of two alternative mating behaviors. Callers maintain territories and vocalize to attract females. Other males act as satellites: they remain silent and wait near callers, and then attempt to mate with females approaching the caller. The mating success of callers usually exceeds that of satellites, with callers obtaining up to 92% of the matings in some cases (Krupa, 1989). Although some females mate indiscriminately with both satellites and callers, other females avoid the mating attempts of satellites (Howard, 1988; Krupa, 1989; Sullivan, 1983).

There is significant inter- and intraspecific variation in the extent to which males adopt calling and satelliting. Callers have greater mating success than satellites, but they also face greater costs: calling is energetically expensive and may attract predators. Males have been observed switching between the two behaviors within the same breeding season or even in the same night (Krupa, 1989; Perrill et al., 1982; Sullivan, 1983, 1989). In some populations, callers are larger than satellites (Fairchild, 1984; Gerhardt et al., 1987; Sullivan, 1983). In other populations, there is no size difference (Lance and Wells, 1993; Sullivan, 1989). These results suggest that in some populations a male's success for a given behavioral strategy may depend on his size or energy reserves. The frequency of satellites may also be positively correlated with the density of callers (Krupa, 1989; Sullivan, 1982a). However, some anuran breeding aggregations consist solely of calling males (Cherry, 1993; Sullivan,1982b).

We developed a model focused primarily on factors potentially influencing anuran breeding phenology given the basic breeding system. We were able to compare our results with those of an earlier model of anuran breeding behavior (Lucas et al., 1996). However, we reduced the number of factors involved, and thus we also evaluated the level of complexity necessary to generate observed anuran breeding phenologies in those species where weather does not limit the breeding season. We also explored how predation risk and foraging success affect the structure of the breeding season. A variety of other factors, including the distribution of initial male states, the length of the breeding season, and the probability of a lone male obtaining a mate, were also manipulated to evaluate the sensitivity of our model.

METHODS

We used a dynamic optimization approach to model the sequence of decisions an animal must make to maximize expected lifetime reproductive success. With each decision, the state of the animal is altered, influencing the choices it makes in the future. Dynamic optimization predicts time-specific optimal decisions for each level of a state variable, X, at a given time, t. The model is solved by iterating backward through time, evaluating the fitness outcome of each alternative action given the current state and assuming subsequent behavior maximizes fitness. The result is a matrix of optimal decisions for each $X(t)$. Furthermore, we can use this matrix to describe the trajectory from time 0 to T (the time horizon) for an individual starting at any particular state (Mangel and Clark, 1988).

We incorporated a game component using the approach outlined by Houston and McNamara (1987). Their "playing the field" formulation consists of solving a simple dynamic optimization model and then using forward iteration to predict the population distribution of states and behavior given the optimal state-dependent decision matrix from the model. The population distribution of states and behavior then determines the benefits and/or costs associated with alternative behavior, and the simple dynamic optimization model is rerun with these new parameter values. An evolutionarily stable strategy (ESS) is established if after several iterations, the new mutant strategy is equivalent to the population strategy, so that no alternative strategy can successfully invade the population's strategy (see also Arak, 1988; Maynard-Smith, 1982).

The simple dynamic optimization model

We assumed that male frogs adopt one of four tactics, indexed as i, specified by Lucas et al. (1996): (1) hide, (2) forage, (3) satellite, or (4) call. In the basic model, each time interval, t, corresponds to one night in a potential breeding season of 14 nights ($T = 14$). Energy reserves serve as the state variable, $X(t)$, and take 1 of 16 levels. These levels were arbitrarily designated 1–16. In the basic model, our starting population consisted of an even distribution of males across states. We assumed that individuals died if $X(t) < 1$. In the final time period, expected future reproductive success (Φ, which represented a small probability of surviving to breed in a second season) was a function of state at that time, T:

$$\Phi = 0.011X(T). \quad (1)$$

Each tactic is associated with a unique combination of costs and payoffs (Table 1). We assumed predation risk to be lowest in frogs that hide, higher in those that forage or satellite, and highest in callers. Only foragers could increase their energy reserves, receiving a net increase of 1 energy unit with a probability, f, of 0.4. In addition, only satellites and callers could mate. A lone caller had a fixed probability, 0.005, of mating in any time interval. In the absence of callers, satellites had no probability of mating. As the number of calling males increased, the mating success of each caller was:

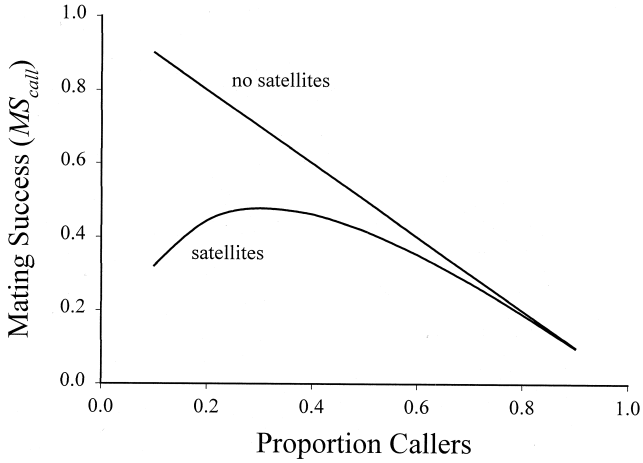

Figure 1
Caller mating success, at a fixed state, as a function of the proportion of callers in the whole population. Shown is the expected mating success of callers in the absence of satellites (i.e., the direct effect of competition among callers) and with variable satellite numbers such that the proportion of satellites = 1—proportion of callers (i.e., in this case the population considered is only those individuals engaged in reproductive activities, calling or satelliting). Caller mating success in the model would fall between these two lines depending on caller-to-satellite ratios.

$$MS_{call}(t) = \frac{1 - c(t)}{1 + \left[\frac{l_{sat}s(t)}{c(t)}\right]} + \frac{0.5X(t)}{16}, \quad (2)$$

where MS_{call} is the mating success of a caller, $c(t)$ and $s(t)$ are the proportions of callers and satellites in the chorus at time t, respectively, and l_{sat} is the probability of a satellite intercepting an incoming female. Thus, the mating success of callers initially increased with chorus size due to the attraction of more females to the chorus, and then decreased due to competition with other callers (Tejedo, 1992; Wagner and Sullivan, 1992). This relationship was adapted from Lucas et al. (1996). However, our model differed from theirs by not explicitly considering the effects of age and weather and by incorporating energy state as a variable that could directly influence caller mating success (e.g., Equations 2 and 4). The addition of energy-state–dependent caller mating success was justified, as female preference for long calls or high calling rates, calling patterns that require increased energy expenditures by males (Bevier, 1997b; Taigen and Wells, 1985), has been demonstrated in several species (Gerhardt, 1991; Passmore et al., 1992; Sullivan, 1983). A logical extension of this result is that males with higher energy states may be able to produce calls that are more attractive to females. Satellites intercepted females, and so increases in the number of satellites decreased each caller's probability of mating (Figure 1). We assumed that the probability of a satellite mating was:

$$MS_{sat}(t) = \frac{l_{sat}}{1 + \left(\frac{l_{sat}s(t)}{c(t)}\right)}, \quad (3)$$

where MS_{sat} is the mating success of a satellite. In this case, as the ratio of satellites to callers increased, the mating success of each satellite decreased due to competition among satellites.

In the initial run of the model, mating success for callers was calculated as a linear function of the male's energy state, $X(t)$, using the equation:

$$MS_{call}(t) = 0.1 + 0.05X(t). \quad (4)$$

The mating success of satellites, MS_{sat}, was set at a constant value of 0.25. After the first iteration, mating success was calculated using Equations 2 and 3.

The generalized form of the dynamic programming equation, which maximizes expected lifetime reproductive success from time t forward given that $X(t) = x$, is:

$$F(x, t, T) = \max_i [MS_i + s_iF(x_i', t + 1, T)] \quad (5)$$

where MS_i is the current reproductive output, s_i is survivorship, and $F(x_i', t + 1, T)$ is the expected lifetime reproductive success given x', the tactic-specific state in time $t + 1$. The fitness associated with each behavioral option differed somewhat, as described below. For those males who hide, the expected fitness is:

$$F_{hide}(x, t, T) = s_{hide}F(x - c_{hide}, t + 1, T), \quad (6)$$

where $F(\cdot)$ is the expected lifetime reproductive success given the state in the next time interval, $x - c_{hide}$, where c is the metabolic cost per time unit of hiding. Hiders acquire neither energy nor matings, so $MS_{hide} = 0$, but they do ensure their survival to the next time interval. Foragers also do not mate, ($MS_{forage} = 0$) but may locate food and increase their energy reserves:

$$F_{forage}(x, t, T) = s_{forage}\{[f \cdot F(x - c_{forage} + y, t + 1, T)] + [(1 - f) \cdot F(x - c_{forage}, t + 1, T)]\}, \quad (7)$$

where f is the probability of finding food, and y is the energetic yield of the food. The first part of the equation corresponds to the case of finding food; the second part of the equation corresponds to the case of not finding food. For satellites and callers, mating success enters into the fitness equation:

$$F_i(x, t, T) = MS_i + s_iF(x - c_i, t + 1, T), \quad (8)$$

with i being either call or satellite.

The dynamic game

We used a game approach to explore male behavior in the model. This approach assumes an initial distribution of male states and assumes that all males adopt the optimal state- and time-specific behavior. Based on the optimal behaviors, we calculated the state transition probabilities between time interval t and time interval $t + 1$. The product of the current distribution of states and the appropriate transition matrix describes the subsequent distribution of states. Thus, we described population distributions of states for all time intervals. Parameters that are influenced by the population were recalculated given the time-specific population distributions, and the original model was rerun with these new parameters. The output at the end of each iteration described the "mutant" strategy with the greatest fitness. The model then assumes that the entire population adopts this strategy and recalculates the population distributions. This procedure was continued until the best mutant strategy was equivalent to the population strategy (Houston and McNamara, 1987; St. Mary, 1997). For our model, this convergence generally occurred after approximately 10 iterations.

Parameter and sensitivity analysis

Manipulations of parameters were performed with two goals in mind: to investigate the effect of varying particular param-

eters on the outcome of the model, and to test the robustness of the model. An additional purpose of this model was to compare the results of our manipulations to those of the Lucas et al. (1996) model, which also used a dynamic-optimization approach to explore chorusing behavior in anurans. Consequently, we adapted some of their model's structure in creating our model, differing primarily at those points where we wanted to direct our investigations. One of the crucial differences between the models is how they address the role of energetics in determining optimal strategies and temporal chorusing patterns. Both models considered how varying the cost of calling can affect chorusing patterns and optimal tactics, assuming that varying calling cost may reflect either differences in physiological costs of calling or in the ability of callers to recoup some of these costs by foraging during the day. However, our model also considered how the environmental resource base of a habitat might affect breeding behavior by varying the probability that a forager will be successful.

We altered the following parameters to explore their effects on optimal strategies: predation risk, s_{call}; foraging success, f and γ; the terminal fitness function, Φ, and the cost of calling, c_{call}. To evaluate the impact of predation on the model's predictions, caller survivorship was varied from 0.99 to 0.81 in decrements of 0.02. At the low end, these levels of within-chorus mortality approximate field estimates (Murphy, 1994). We explored the importance of foraging using two different manipulations. First, the yield from foraging was varied in integer values from 2 to 15 energy units, and second, the probability of obtaining food was varied from 0.1 to 1.0 (in increments of 0.1). The effect of the terminal fitness function was examined by setting terminal fitness to 0, 0.05, 0.1, 0.25, and 0.5 times the terminal state, $X(T)$. Finally, the cost of calling was incorporated into the model as a constant, $c_{call} = 2$, which was later decreased such that $c_{call} = c_{hide}$.

Several manipulations were also performed to test the robustness of the model's predictions. First, a lone caller's probability of finding a mate was set to either 0.05 or 0.1. The effect of the breeding season length was examined by varying the number of available nights from 14 to 21. Finally, the initial distribution of caller states was established as a normal curve with mean = 8 and five different variances, SD = 1.2, 2.0, 2.4, 2.6, and 2.8. These variances fall within a moderate to high range of within-population variation relative to field measurements of male energy reserves, assessed with glycogen or fat-body levels (MacNally, 1981; Wells and Bevier, 1997). We also ran the model using an initial distribution of states with mean = 12 and SD = 2.

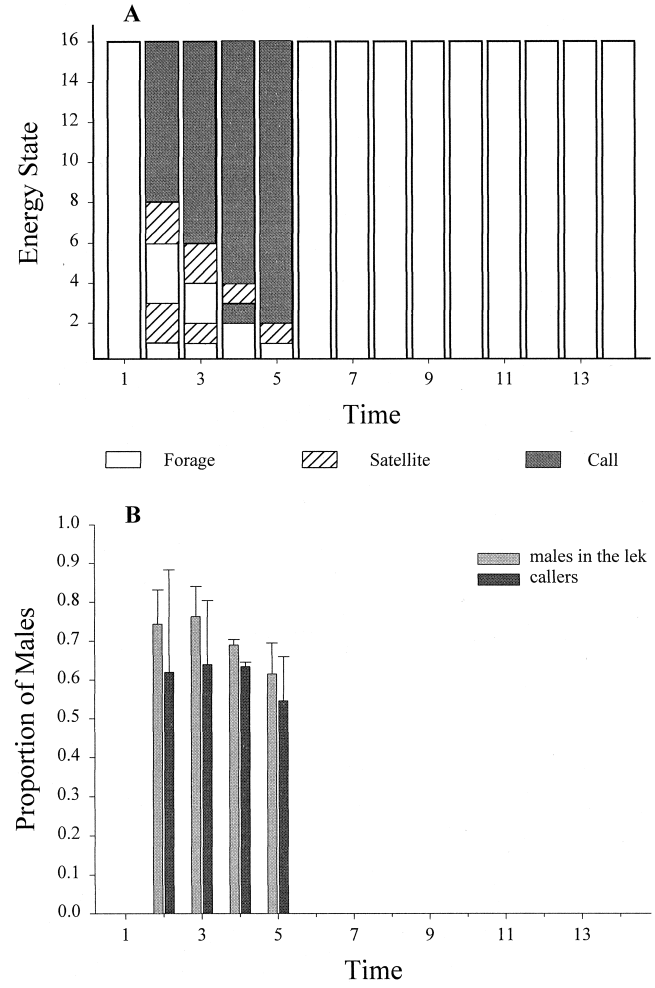

Figure 2
(A) The optimal time- and state-specific decisions predicted by the model using the default parameters (see Table 1) from iteration 20. The optimal decisions predicted from iteration 19 were substantially similar. On nights 2–5 all males with energy reserves ≥ 3 called; on nights 3–5, males with energy reserves of 2 participated in the lek as satellites. (B) The proportion of males in the population participating in the lek in iterations 19 and 20 using the default model parameters. Error bars represent SDs about the mean of two iterations.

RESULTS

By manipulating relatively few parameters (specifically, the probability of finding food and the cost of calling), the model was able to generate all three basic phenology patterns: explosive breeding, prolonged breeding with episodic chorusing, and prolonged breeding with continual chorusing (i.e., explosive). Sensitivity analyses suggested that the qualitative patterns obtained by these manipulations were not affected by changes in other parameters.

Predictions using the initial parameter values

Using the default parameter values, the model predicted a highly synchronized and restricted pattern of chorusing. Males of nearly all states called on nights 2–5 (Figure 2A), resulting in a high proportion of the male population calling on each of those nights (Figure 2B). Males with high initial energy reserves tended to call continuously, depleting their reserves, whereas males with lower reserves tended to alternate between calling, satelliting, and foraging. When males with initially high energy states called for a number of nights and depleted their reserves, they too entered this alternating pattern. Thus, despite our assumption that the environment was conducive to breeding over the entire time frame, chorusing was explosive and occurred only over a few consecutive nights. Males primarily foraged the remainder of nights.

Manipulations of the parameter values

Our goal in manipulating parameters was to explore the circumstances under which explosive versus more extended patterns of reproductive activity were obtained. We also examined patterns of satelliting and calling for comparison to the model of Lucas et al. (1996). We manipulated predation risk (s_{call}), as well as the probability of finding food when foraging (f), the terminal fitness (Φ), and the probability of attracting a mate in the absence of other calling males. For the purpose of characterizing the predicted patterns of chorusing more

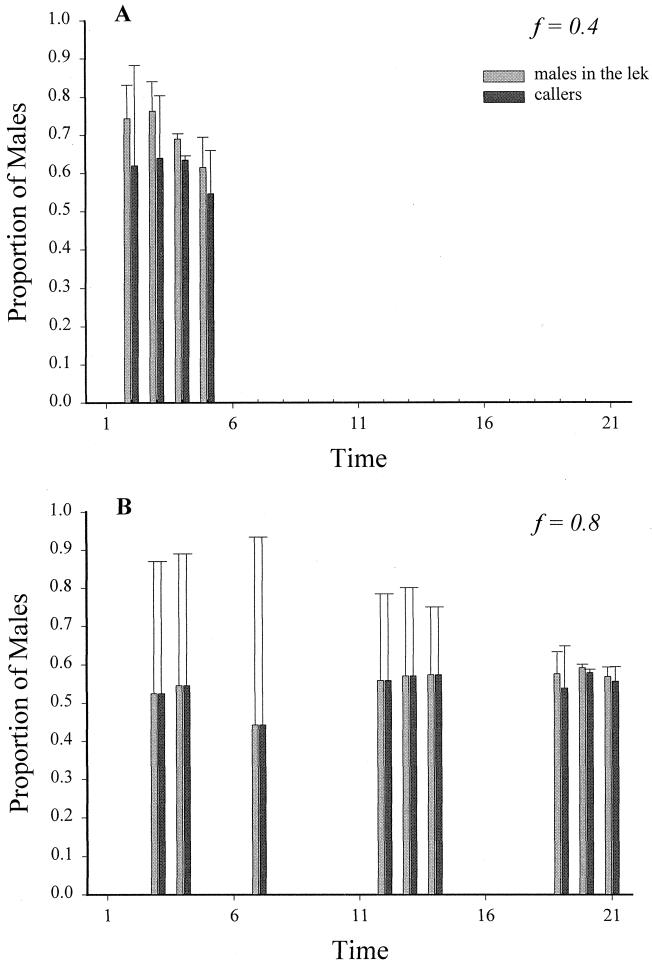

Figure 3
The proportion of males in the population engaged in reproductive activities (both the total proportion of males in the lek and the proportion of males calling) on each night of the potential breeding season, as predicted from iterations 19 and 20. Error bars represent SDs about the mean of two iterations (as in Figure 2). (A) The probability of finding food = 0.4. (B) The probability of finding food = 0.8.

fully, we expanded the time horizon (T) for these manipulations to 21 nights. This change had no effect on the chorusing pattern predicted with the default parameter values (compare Figures 2B and 3A).

Changes in predation risk to callers had little effect on the pattern of calling. Over the range of survival probabilities (s_{call} = 0.81–0.99; the latter representing decreased survivorship of callers), the predicted pattern of chorusing remained explosive. Increased predation risk to callers constricted the breeding period (4 nights when s_{call} = 0.99, 2 nights when s_{call} = 0.81). When terminal fitness was also increased, predation risks on the order of 0.81 resulted in the suspension of breeding entirely. The occurrence of the satelliting tactic was likewise unaffected. Under all predation regimes, satellites occurred most frequently in the lowest energy state classes (x = 2 and 3 generally, but occasionally values of x as high as 8). This result remained unchanged from the default model predictions (Figure 2A). Thus, predation risk can influence breeding patterns to a certain extent; however, in the context of our model, it was not sufficient to explain the variation in explosive versus protracted breeding or the frequency of satellites.

The probability of finding food, on the other hand, was a critical parameter in shifting between predicted patterns of explosive and protracted breeding. When the probability of finding food was <0.6, explosive breeding occurred (Figure 3A). However, with higher probabilities of finding food, chorusing occurred in repeated bouts over the course of the potential breeding season (Figure 3B). These patterns held as the potential breeding season was extended (note T = 21 for Figure 3). The optimal state- and time-specific decision for f < 0.6 included satellites in essentially the same pattern as the default model (Figures 2A and 3A). However, when $f \geq 0.6$, satellites were rare, occurring only in the last few nights of the potential breeding season and only at the lowest energy state participating in the chorus (i.e., states 2–5, depending on the precise value of f). Interestingly, the yield attained if food is found (y), did not affect the breeding phenology and only marginally affected the pattern of satelliting. We varied the foraging yield from 2 to 15 energy units; when yield was ≥8 energy units, satelliting no longer appeared in the optimal decision set. Thus, breeding phenologies are predicted to be more explosive and satellites more common as food limitation increases.

Although we varied several other parameters, cost of calling was the only other parameter that significantly affected breeding phenology. Specifically, for a fixed value of the probability of finding food (f), lower costs of calling (i.e., $c_{call} = c_{hide}$) increased the duration of chorusing bouts (compare Figure 3 with Figure 4). Even when the probability of finding food was low, the predicted pattern of calling was continuous and more extended (compare Figures 2B and 3 with Figure 4A–C). With no cost of calling, the model predicted continuous chorusing for 12 nights, regardless of the length of the potential breeding season. When the potential breeding season was extended (T = 21) and the probability of finding food was high, chorusing again became episodic (Figure 4D). Our interpretation of these results is that the chorusing generally continues until energy reserves are exhausted. Thus, as the number of energy states increases and the cost of calling is reduced, the number of nights calling may be extended. However, if the breeding season is sufficiently long and the probability of finding food is high, males alternate synchronously between calling and foraging. Furthermore, when there is no additional energetic cost of calling, satelliting disappears entirely from the optimal decision set, as would be expected.

Variation in the initial distribution of male states in the population had relatively little effect on breeding phenology. Generally speaking, with a mean male energy state of 8 in the population, as the standard deviation about that mean decreased, the number of nights chorusing declined (e.g., with SD = 2.0 chorusing was reduced to 2 nights). Conversely, increased variation in male states increased the number of nights on which chorusing occurred, but did not change the qualitative results. This effect was more pronounced when predation risk to callers increased.

DISCUSSION

Male strategies

Previous models have examined alternative male mating tactics in anurans (Lucas and Howard, 1995; Lucas et al., 1996; Waltz, 1982). The model by Lucas et al. (1996) explicitly considered energy state in determining the optimal strategy. It predicted that age and energy state of males participating in the chorus, density-dependent factors, and weather influence mating strategy. Our findings largely support these hypotheses, although our model is not as complex. Both models found that increasing the cost of calling caused males to switch from

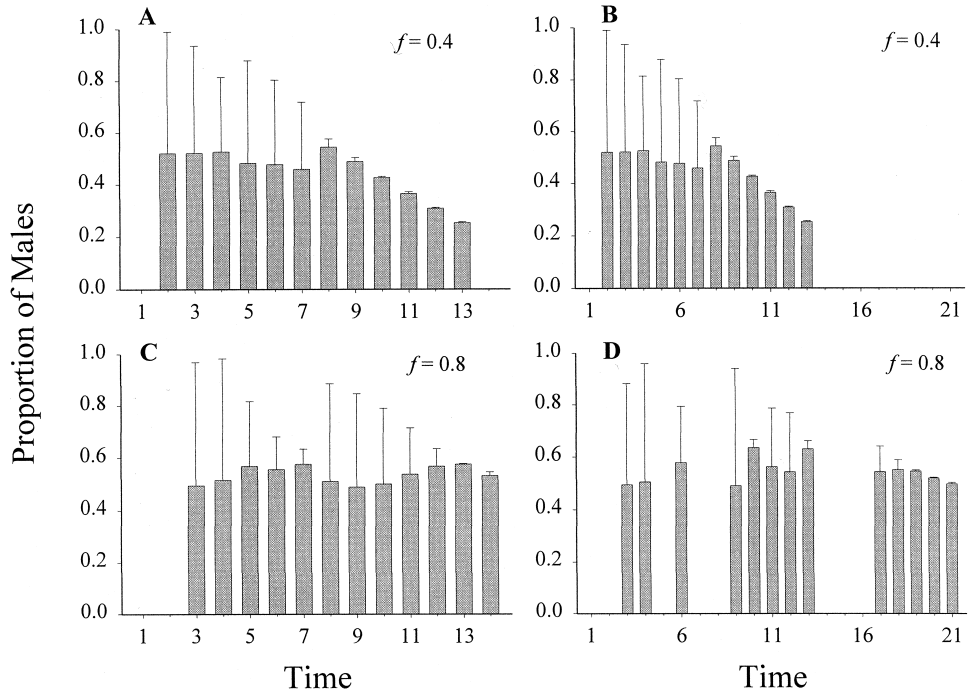

Figure 4
The proportion of males participating in the lek on each night of the potential breeding season. The effect of reducing the cost of calling with a low probability of finding food, (A) and (B); and with high probability of finding food, (C) and (D). Panels A and C represent the predicted chorusing patterns given a short potential breeding season (T = 14); (B) and (D) represent the predicted chorusing patterns given an extended season (T = 21).

calling to satelliting and that individuals foraged as their probability of surviving to another breeding season increased. Additionally, when the terminal fitness function equaled zero, satelliting was dropped from the behavioral repertoire. Lucas et al. (1996) also found that first-year males did not chorus as often and were more likely to become satellites than second-year males. Together, these results suggest that the probability of an individual surviving to another breeding period is a significant determinant of his mating strategy. Specifically, energetic constraints may determine male strategies not because males become incapable of calling but because calling may decrease lifetime reproductive success by decreasing the probability of an individual surviving to another season.

Breeding phenology

The primary goal of our model was to evaluate what factors affect anuran breeding phenology. By manipulating only a few parameters related to the energetics of calling males, our model was able to produce all breeding patterns observed in anuran reproduction: explosive, synchronized breeding periods as well as extended breeding periods with either continuous or intermittent calling.

In our model, the temporal patterns of reproduction remained relatively stable in response to manipulations of several parameters initially expected to affect breeding phenology. Varying the probability of surviving to subsequent seasons had little impact except at extreme levels. When the probability of surviving was high, reproduction was foregone entirely. Conversely, when there was no probability of surviving, the length of the breeding season increased, although it did not occupy all available nights. The Lucas et al. (1996) model found that either a high probability of a satellite successfully intercepting a female or a high risk of predation for callers produced explosive breeding. This was not found in our model. Although low caller survivorship did condense the breeding period by a few days, it did not result in explosive chorusing. Low caller survivorship in our model either produced shorter calling periods within a prolonged episodic season or reduced the length of an explosive season, depending on the phenology generated by other factors in the model. In addition, extremely high caller survivorship, equivalent to that experienced by foragers or satellites, did not prolong the breeding season.

In contrast, significant qualitative changes in the predicted breeding phenology of our model were associated with varying the probability of successful foraging. At low probabilities of finding food (< 0.5), all reproductive activity was confined to a single, explosive period with most of the population participating as either callers or satellites. In contrast, when the probability of finding food was relatively high ($f = 0.6$), the breeding season expanded and consisted of multiple chorusing bouts punctuated by foraging periods, a pattern similar to many prolonged breeders (Donnelly and Guyer, 1994; Green, 1990; Sullivan, 1992; Tejedo, 1992). These results suggest that when resources are limited or patchy, other extrinsic factors may not be necessary for explosive breeding to occur.

Reducing the cost of calling to that of hiding also influenced the temporal pattern of reproduction. With a low cost of calling, populations with both high and low probabilities of successful foraging bred synchronously in a single, continuous chorus. The duration of this chorus (12 days) was considerably longer than the chorus generated when the cost of calling was greater (4 days; Figure 4). When the potential breeding season was expanded and the probability of successful foraging was low, the chorus duration remained 12 days. This precise chorus length may be a function of the magnitude of the maintenance cost relative to the range of potential energy states in our model. Nonetheless, these results reflect the qualitative effects of varying the cost of calling. Bevier's (1997a) work examining chorus tenure and calling rate in two species of hylids, *Scinax rubra* and *Scinax boulengeri,* supports our findings. *Scinax rubra* has a higher call rate, calls for more hours per night, and presumably has a higher calling cost than *S. boulengeri.* Accordingly, *S. boulengeri* breeds continuously and has much longer chorus tenures than *S. rubra.* However, it is also important to note that in our model, when the potential breeding season was expanded and the probability of finding food was high, chorusing was episodic and punctuated by foraging activity despite a low calling cost. This

suggests that variation in resource availability may shape breeding phenologies regardless of the energetic cost of calling.

Our model suggests that it is the probability of finding food that determines chorusing pattern rather than energetic constraints produced by low but reliable foraging yields. Increasing the potential yield to half that of the highest possible energy state lengthens the breeding season slightly but does not affect the patterns of explosive breeding at low probabilities of finding food and prolonged episodic breeding at higher probabilities of finding food. Murphy's (1994, 1999) studies of the determinants of chorus tenure in a prolonged-breeding frog, *Hyla gratiosa,* support our findings. He found that males that were fed as they left a chorus returned sooner and stayed in the chorus longer than unfed males. The amount fed, however, did not significantly affect the timing of their return or their subsequent chorus tenure. Patterns of resource distribution may therefore have a greater affect on breeding phenology than absolute resource abundance. An unpredictable and patchy distribution of resources may produce an explosive phenology even when prey, once captured, are highly energetically profitable.

These results suggest two nonexclusive hypotheses about the role of resource availability in determining the breeding phenology of anuran populations: a starvation minimization strategy and an energy-state maximization strategy. In resource-limited or patchy environments, the probability of starvation increases, and foraging becomes increasingly significant in determining the lifetime fitness of an iteroparous organism. Thus, individuals have to forage more to decrease the probability of starvation. The starvation minimization strategy is to restrict reproduction to a few days in the potential breeding season when the presence of other callers increases the probability of reproductive success, and then to spend the remainder of the potential breeding season foraging. In contrast, if the probability of a forager increasing its energy state is high and energy state is positively related to reproductive success, the optimal behavior may be the energy-state maximization strategy in which calling is interspersed with foraging. There is considerable evidence that this occurs in some prolonged breeders as males move in and out of the chorus throughout the season (Krupa, 1989; Murphy, 1994; Sullivan, 1982b, 1992). Under these conditions, foraging itself is a reproductive activity (Abrams, 1983, 1991).

Our model does not consider the physiological adaptations anurans may possess to fuel calling under conditions of low resource availability. For example, wood frogs (*Rana sylvatica*) and spring peepers (*Psuedacris crucifer*) frequently inhabit the same ponds. Both begin calling in the spring at similar times; however, wood frogs are explosive, 3- to 5-day breeders, whereas spring peepers breed for up to 2 months (Wells, 1977). It appears that these frogs face a seasonal gradient in resource availability with resources limited at the outset of the season (Wells and Bevier, 1997). Spring peepers have substantial lipid reserves that allow them to pass through the period of limited resources and extend their breeding season as resources increase. In contrast, wood frogs do not have lipid reserves and may breed explosively because of constraints imposed by the interactions of physiology, calling energetics, and a resource-limited environment (Wells and Bevier, 1997). This example highlights the need to consider not only the interactions between resource availability and breeding phenology, but also the adaptations species possess to overcome resource constraints.

Few data exist that would allow us to test the hypothesis that explosive breeding is more prevalent in resource-limited or unpredictable, patchy environments. Some anuran species, including *Bufo woodhousii* and *Bufo americanus,* include both explosive and prolonged breeding populations (Fairchild, 1984; Howard, 1988; Sullivan, 1989, 1992). Such species provide an excellent opportunity for examining the hypotheses developed here. Additionally, both explosive and prolonged breeders inhabit some permanent habitats. Comparisons of the degree of resource specialization, foraging efficiency, competitive ability, and seasonal variations in resource abundance for these species would allow a critical assessment of the hypothesis that breeding phenology is related primarily to resource availability.

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